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The conservation biology and ecology of the African leopard *Panthera pardus pardus*

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Abstract

The African leopard *Panthera pardus pardus* is an apex predator, and a reliable indicator of a healthy ecosystem. Currently assessed as 'near threatened' by the IUCN Red List of Threatened Species, leopards are exposed to a range of threats that include: habitat loss and/or degradation, depletion of natural prey, conflict with people, consumptive- and non-consumptive practices, and the illegal trade of leopard products.

Leopards have disappeared from 37% of their historical range, and are continuing to decline. Leopards have been extirpated across many areas of Africa, especially where people are densely populated, which has left patchily distributed leopard populations throughout the continent—to date, an accurate census has never been achieved.

A variety of management techniques and conservation schemes are used in an attempt to mitigate threats directed at leopards; for example: (1) improved livestock husbandry that reduces livestock depredation and thus reduces retaliatory killing of the supposed offender—often thought to be the leopard, (2) designing community-based conservation schemes that benefit local people (*i.e.*, food, money, jobs, ownership), (3) financial compensation for livestock losses, (4) ecotourism and regulated sport hunting, and (5) ratification of conservation-orientated government policies.

Detailed, long-term leopard research began in the 1970's, and continues to the present day with many peer-reviewed papers focusing primarily on their ecology within savannah ecosystems. Technological advances (*e.g.*, GPS tracking collars and remote camera traps) are helping to further our knowledge of leopard demographics, intra- and inter-specific interactions, predation, habitat use, and effective monitoring techniques. Nevertheless, more research is desperately required if leopard populations are to persist within human-dominated landscapes, like continental Africa.

Keywords: human-wildlife conflict, predator, bushmeat, keystone species, top-down control, umbrella species, felid, conservation, carnivore

The importance of carnivores

The integrity of ecosystems throughout the world are often dependent on the functional presence of carnivores (Soulé and Terborgh, 1999). Many carnivores are capable of altering trophic structure and biodiversity through process known as top-down control (Elmhagen and Rushton, 2007). This phenomenon occurs when carnivores are able to prevent the proliferation of herbivores that would otherwise significantly reduce plant biomass through increased grazing pressure (Miller et al., 2001). For example, overexploitation of sea otters *Enhydra lutris* in the north Pacific due to the demand for fur led to increased marine invertebrates which devastated kelp forests, this led to a reduction in fish, bird and invertebrate diversity (Eates and Duggins, 1995).

Carnivores can provide ecological boundaries that protect weaker competitors from competitive exclusion by predating on—or altering the behavior of—superior species (Miller et al., 2001). Some carnivores are regarded as ‘keystone species’ due to the enormous ecological effects they impose on other individuals and ecosystems (Eates et al., 2001). The impact of carnivores is therefore not only limited to predation, but include indirect effects that cascade through different trophic levels (Miller et al., 2001).

Carnivore intraguild interactions are also negatively affected by the removal of top predators allowing for outbreaks of mesopredators, known as ‘mesopredator release’ (Caro and Stoner, 2003; Ritchie and Johnson, 2009). An escalating mesopredator population puts increased pressure on smaller prey species (Ritchie and Johnson, 2009). For example, within a fragmented Californian landscape, the reduction of coyotes *Canis latrans* as a result of intensive urbanization led to an increase in smaller carnivores. These mesopredators over-exploited scrub-breeding bird populations which led to an overall decline in local bird diversity (Crooks and Soule, 1999).

Prey species have adapted as a result of carnivory by evolving morphological, physiological and behavioural traits that help reduce the risk of predation (Logan and Sweanor, 2001). It is hypothesized that ancestral hominids evolved—in part—by scavenging on predator kills. This essential food source was necessary for the development of a complex neural system, which could have been a key factor enabling hominids to progress into temperate regions (Blumenschine, 1991; Aiello and Wheeler, 1995; Logan and Sweanor, 2001).

Large carnivores are commonly used as ‘umbrella species’ when allocating conservation areas (Andelman and Fagan, 2000). Due to the large spatial requirements of large carnivores, protecting them may ensure that sufficient habitat is protected for other species (Balme, 2009). Additionally, charismatic carnivores act as ‘flagship’ species for non-Governmental organisations and conservation programs wishing to entice public interest (Caro, 2003).

Leopards are indicators of healthy ecosystems (CoP-13, 2004). However, little is known about the impact leopards have on ecosystems, herbivores, predators, mesopredators and even other leopards. These data are required, alongside sound conservation strategies, in order to determine the leopard’s true ecological importance.

Conservation of leopards

Current threats

Predators and humans often compete for limited resources such as food and habitat (Jorgenson and Redford, 1993; Ray, 2001; Treves and Karanth, 2003). Habitat loss and the depletion of prey by people are primary drivers that endanger current leopard populations. In the Congo Basin, leopard populations closer to human communities are significantly smaller or completely absent than that of more remote areas. This decline is correlated with the depletion of natural leopard prey as a result of bush meat hunting which occurs more intensely nearer to human settlements (Henschel et al., 2011).

An expanding human population coupled with the resource requirements of carnivores (*i.e.*, large territories) inevitably leads to human-carnivore conflict (Woodroffe, 2000). Leopard populations are increasingly threatened by ranchers trying to protect livestock (Nowell and Jackson, 1996). The frequency and severity of livestock depredation by leopards depends on the availability of natural prey and the quality of local husbandry practices (Ray et al., 2005). For example, a ranch in northern Kenya that practiced sub-standard husbandry techniques found that 16.4% of livestock losses ($n = 258$) were attributed to leopard predation, in contrast, on a ranch in southern Kenya where herdsman accompanied livestock and prey were abundant, no livestock losses ($n = 433$) were blamed on leopards (Mizutani, 1999; Patterson, 2004). Leopards are often persecuted on the basis of a real or perceived threat they pose to livestock and people, which leads to indiscriminant killing or translocation of the supposed offender (Balme, 2009).

Consumptive practices like trophy hunting significantly depletes local leopard populations—particularly when unregulated (Packer et al., 2009; Packer et al., 2011). Male leopards are the most desired predator trophy in Africa, however, sex determination during hunts is not straightforward and can cause in high female mortality (Spong et al., 2000). In Tanzania, 77 leopard trophies were genetically analyzed to find that 29% were female (Spong et al., 2000). Additionally, a deficiency of male leopards—from trophy hunting—could cause a loss of genetic variation due to a declining population size resulting from a skewed sex ratio (Spong et al., 2000). Leopards show a high dependency for stable, long-term relationships (Bailey, 2005). Increased male mortality disrupts leopard social structure and spatial dynamics (*i.e.*, territoriality), which can lead to increased intraspecific strife and infanticide (Wielgus and Bunnell, 2000; Stoner et al., 2006). In 2008, growing demand by hunters and consumers resulted in an increase in national Convention of International Trade in Endangered Species (CITES) hunting quotas from 75 to 150 leopards per year for South Africa (Balme, 2009).

Translocations of leopards increases social flux by upsetting stable population dynamics (Athreya et al., 2011). Translocation programs in South Africa, and other African countries, are indiscriminately permitted by law (Ray et al., 2005). These individuals undergo extreme stresses once released outside of familiar habitat and often successfully navigate back to their original home ranges. Complex social and ecological processes are at play when top predators—like leopards—are translocated. These processes are barely understood and require further research if this technique is to be considered a viable management option (Athreya et al., 2011).

It is very difficult to confine leopards within protected areas (Balme et al., 2007), and though attempts have been made to construct 'predator proof electric fences' (du

Plessis and Smit, 2001), complete control over the movements of leopards is impossible. As a result, leopards within protected areas often move into landscapes dominated by people. The consequence of this often ends in human-carnivore conflict, and a phenomenon known as the 'edge effect' (Balme et al., 2010). Humans are the primary cause of mortality in large carnivore populations within protected areas, with most deaths occurring when carnivores move beyond reserve boundaries (Loveridge et al., 2007). The peripheries of protected areas act as population sinks that may lead to the decline or extinction of carnivore populations, especially when immigration and reproduction at border regions are unable to balance mortality (Woodroffe and Ginsberg, 1998).

The illegal trade of leopard parts is widespread—occurring throughout Africa and internationally (Ray et al., 2005). For example, French military personnel in Djibouti are a major conduit for smuggling skins into Europe, and in Africa locals sell huge quantities of leopard parts in open tourist markets (Künzel et al., 2000; Shipp, 2002). Additionally, in central and west African countries leopard parts are valued for traditional rituals (Henschel and Ray, 2003). Illegal trade is less common in southern Africa but does still occur; in 2004, 58 leopard pelts were seized in Kwa-Zulu Natal destined for international markets (Hunter et al., in press). The illicit trade and killing of leopards throughout Africa goes mostly unrecorded and are not incorporated into the CITES quota system (Balme, 2009).

Methods used to conserve leopards

The sustainable conservation of wildlife will only be successful if the value of those conservation efforts outweigh the costs and outcompetes alternative land uses that contribute to human welfare (Lindsey et al., 2005). Due to a growing human population, the creation and/or expansion of protected areas is unlikely, emphasizing the need to steer conservation efforts towards enhancing compatible coexistence between people and wildlife (Balme, 2009).

Livestock depredation is seen as a primary area of concern for leopard conservation (Ray et al., 2005). Improvements in livestock husbandry have shown to greatly reduce depredation, simply by guarding livestock by day (Odden et al., 2002), corralling stock at night in well-constructed enclosures with watchdogs (Ogada et al., 2003), and by synchronizing calving periods (Linnell et al., 1996). More technologically advanced solutions range from electric fences (Bourne, 2002), chemical repellants like toxic predator collars (Savarie and Sterner, 1979), carnivore reproductive control using antifertility agents (Tuytens and Macdonald, 1998), and conditioned taste aversion (Shivik, 2006). Lethal measures can be an appropriate method of carnivore control in circumstances where human costs cannot be resolved. This method could deter persecution of predators by appeasing local attitudes and provide hunting revenue or meat to local communities. The elimination of some problem individuals may select for conspecifics that avoid people and property (Treves and Naughton-Treves, 2005). Lethal control strategies must be highly selective (*i.e.*, killing the actual offender) otherwise counter-intuitive results may occur. For example, in Belize, pre-emptive killing of jaguars created livestock predators (Rabinowitz, 1986), similarly, lamb depredation by coyotes in California increased during non-selective coyote control than during selective control (Blejwas et al., 2002).

Financial compensation for livestock losses can be used to mitigate aggressive public perceptions towards leopards (Nyhus et al., 2005). However, compensation schemes

can be extremely expensive, are sensitive to corruption, and in some cases even depress wildlife stock value or accelerate extinction of local species (Rondeau and Bulte, 2007). If handled correctly, financial compensation can be used successfully in areas where people are open to the idea. For example, financial incentive programs such as 'Snow Leopard Enterprises' in Mongolia allow scientists to provide skills training to locals which has resulted in a 25% increase in per capita income per household, in exchange, locals commit to snow leopard *Panthera uncia* conservation initiatives (Mishra et al., 2003). In the Waterberg region of South Africa, Swanepoel (2009) found that 79% (n = 57) of livestock ranchers would consider participating in leopard based conservation initiatives—with 15% interested in economic incentives. These statistics highlight the opportunities available for conservation programs wishing to use financially based reward systems.

Ecotourism and regulated sport hunting can be used to generate local and regional revenue. Communities may feel that the costs of living with carnivores are offset by the financial benefits brought about by their conservation (Hutton and Leader-Williams, 2003). In a Namibian community, leopards were responsible for livestock loss totaling N\$55 (N\$ = £0.10) per village per year. This prompted an ecotourism solution, whereby locals would guide tourists to view leopards in the wild, generating N\$667 per village per year (Stander et al., 1997). Sport hunting is the most profitable form of consumptive wildlife utilization, and is a growing industry in Africa (Child, 2000), generating US\$ 65.6–137 million per year in South Africa (Damm, 2005). Leopards are the second most desired trophy species in Africa, after buffalo, and hunters have shown considerable interest in hunting where conservation objectives are met, indicating that client preference could positively assist conservation efforts (Lindsey et al., 2006).

Local authorities play a large role in leopard conservation as they govern the capture and translocation of leopards, lethal control of problem individuals, and CITES quota restrictions (Ray et al., 2005). However, these decisions are primarily based upon unsound scientific findings (Balme, 2009). In response to these shortcomings, pioneering scientific research based in Phinda Private Game Reserve, Kwa-Zulu Natal, South Africa, have prescribed management strategies for local authorities that successfully increase the viability of local leopard populations (e.g., decreasing annual leopard mortality, reducing human-leopard and intraspecific conflict, and an increasing leopard reproductive output). These policies are to be ratified in other provinces across South Africa, and further north into the African continent (Balme et al., 2009b).

Leopard populations are extremely difficult to count. Their wide-ranging movements, nocturnal habits, solitary nature and naturally low densities confound monitoring efforts (Balme et al., 2009a). Obtaining reliable population estimates for wildlife is often achievable through aerial censuses, road-strip (*i.e.*, viewing wildlife from vehicles) and complete counts (Redfern et al., 2002; Balme et al., 2007). However, these techniques are impractical, expensive, and time-consuming due to the leopard's cryptic nature (Balme et al., 2009a). Alternative sampling methods have been developed to estimate abundance or provide indices of relative abundance (Williams et al., 2002). Track count monitoring is useful, but requires highly trained trackers and suitable substrate for the identification of individual track imprints (Hayward et al., 2002; Karanth et al., 2003). A method developed by Karanth & Nichols (1998) using camera trapping capture-recapture models to estimate tiger *Panthera tigris* population size have subsequently been used for a range of felid species, including leopards, with excellent results (Jackson et al., 2006; Henschel, 2008; Balme et al., 2009a).

Distribution and the conservation status of the African leopard

African leopards are normally associated with mountainous areas, woodland savannah, and forest ecosystems but also inhabit deserts where they are restricted to watercourses (Nowell and Jackson, 1996). The only habitat not able to support leopards are barren sand dune systems (Swanepoel, 2009). Leopards are capable of surviving at sea level to as much as 4,600 m (Hunter et al., in press). Ray, Hunter & Zigouris (2005) estimate that leopards have disappeared from over 37% of their historical range—with South Africa, Nigeria and the Sahel belt containing the most depleted populations (Henschel et al., 2008). They are thought to be extinct in Zanzibar and possibly extinct in Egypt (Hunter et al., in press). Leopard extirpation has occurred in many areas across Africa, especially where people are densely populated, which has left patchily distributed leopard populations throughout the continent.

Early attempts to taxonomically classify the leopard were carried out in the 1930's. Twenty-seven subspecies were named, based on their distribution, varied coat patterns and morphological characteristics (Pocock, 1930; Pocock, 1932). In 2001, Uphyrkina et al. (2001) reduced these subspecies to nine discrete populations, namely; *Panthera pardus pardus* (Africa), *P. p. nimr* (Arabia), *P. p. saxicolor* (Central Asia), *P. p. fusca* (India), *P. p. kotiya* (Sri Lanka), *P. p. delacouri* (South China), *P. p. japonensis* (North China), *P. p. orientalis* (Russian Far East) and *P. p. melas* (Java).

African leopards were the first group to split from the phylogenetic tree. Their departure corresponds in time with the postulated migration of modern humans out-of-Africa (Ingman et al., 2000; Uphyrkina et al., 2001). As a result of their broad habitat tolerances and wide distribution, leopards show higher genetic diversity than other felids such as lion, cheetah (Driscoll, 1998), jaguar (Eizirik et al., 2001) and puma (Culver et al., 2000). Additionally, African leopards possess the broadest range of genetic variation of all the *P. pardus* subspecies (Uphyrkina et al., 2001).

Estimating leopard numbers in Africa has been attempted six times (Myers, 1976; Teer and Swank, 1977; Eaton, 1978; Hamilton, 1981; Martin and de Meulenaer, 1988). The most recent estimation by Martin & de Meulenaer (1988) state up to 714 000 leopards live in sub-Saharan Africa. However, this estimation has been criticized for its inaccuracy and over simplicity (Norton, 1990). All attempts to estimate leopard numbers have been criticized for various reasons, therefore the number of African leopards still eludes researchers (Nowell and Jackson, 1996). Nevertheless, leopard populations are decreasing in Africa (Henschel et al., 2008), whilst Indian populations (*P. pardus fusca*) are believed to be increasing (Singh, 2005).

Leopards are included within CITES Appendix I, with legal international trade limited to exporting skins and trophies (Henschel et al., 2008). Thirteen African countries are permitted to trade in leopard products under the CITES quota system, 11 of which support leopard hunting (Ray et al., 2005; Henschel et al., 2008). The latest CITES export quotas for leopards combined for all African states was 2658 in 2008 (CITES, 2008). Leopards have recently been placed in the 'near threatened' IUCN red list category, however their status is to be reevaluated to 'vulnerable' in the near future given the mounting pressure people are placing on leopards throughout the world (Henschel et al., 2008).

Leopard research

Main areas of research

Research on Felidae is extensive and mostly orientated towards the larger species. A literature search of the world's cats, conducted by Brodie (2009) from 1986–2007, found a total of 2462 papers (966 papers were in situ, where publications dealt solely with the species in question). His findings suggest that more research on smaller bodied cats is required, but also, more emphasis on research that can be applied to other felids is essential.

Detailed, long-term leopard research began in the 1970's and 1980's in the Kruger National Park, the Kalahari desert (Bothma and Le Riche, 1984; Bailey, 2005) and in Kenya's Serengeti National Park (Bertram, 1974). Early studies focused on the ecology of leopards, particularly their spatial requirements and feeding habits, but also on behaviour such as scent-marking and hunting efficiency (Bothma and Le Riche, 1995; Bothma and Coertze, 2004). As scientific interest in leopards began to increase, studies in central Africa began assessing their dietary preference (Hoppedominik, 1984) whilst in Sri Lanka, Santiapillai, Chambers & Ishwaran (1982) documented the bleak status of the leopard in Ruhuna National Park. Further baseline information regarding mountain leopards in the Cape Province of South Africa were published, supporting the findings of Bothma & le Riche (1984) that leopard home ranges are very large (males: 487–2000 km²) particularly in regions with low prey abundance (Norton and Lawson, 1985). Research regarding the distribution of leopards in the Far-East (Pikunov and Korkishko, 1985), their physiology (Abbasi and Braunitzer, 1985; Ahmed et al., 1988), genetics (Roychoudhury and Acharjyo, 1984) and the status of captive leopards throughout the world's zoos (Shoemaker, 1985) were examined during the mid-1980's. Nearing the end of the decade, studies on leopard behavioural ecology in sub-Saharan Africa were increasing with research undertaken in the Orange River Basin and on private game reserves (Tilde and Tilde, 1988; Leroux and Skinner, 1989).

By the 1990's extensive criticism of Martin & de Meulenaer's (1988) African leopard population model had been published (Norton, 1990; Jenny, 1996). Leopard publications began to increase during the mid-1990's (Fig. 1). Research on prey preference and feeding habits of leopards were conducted across the species' range including less studied mountainous ecosystems (Cavallo, 1991; Grimbeek, 1992; Johnson et al., 1993; Stuart and Stuart, 1993). Veterinary research on leopards, and other felids, increased during this period, investigating aspects like the spread of canine distemper virus (Appel et al., 1994; Harder et al., 1996), parasitology (Patton and Rabinowitz, 1994; Pozio et al., 1997), physiology (Macdonald and Johnstone, 1995; Ray et al., 1996; Ray et al., 1997; Stander, 1997), bacteriology and genetics (Miththapala et al., 1996; Thorel et al., 1998).

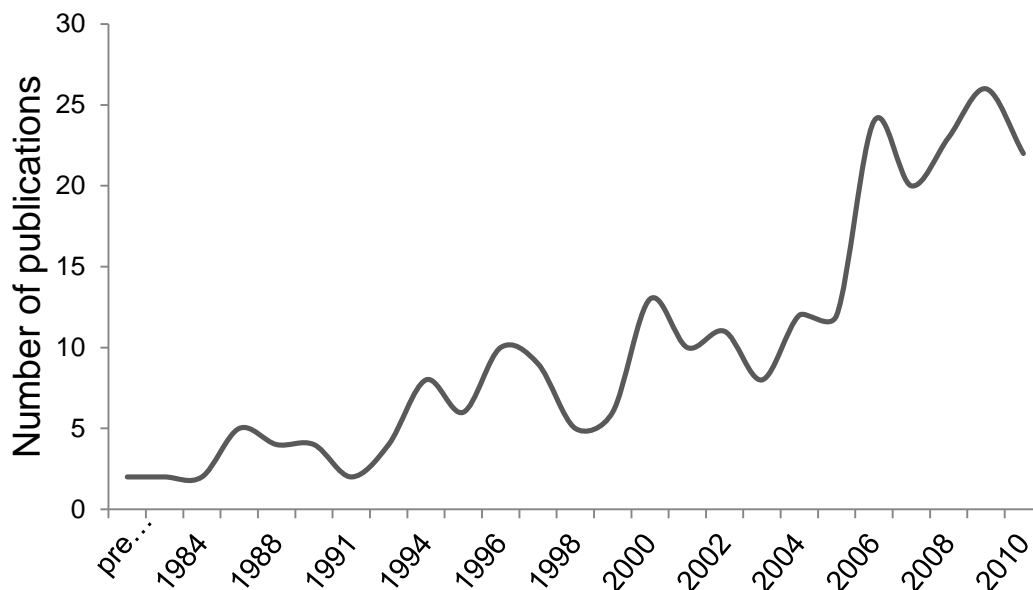


Figure 1: Number of publications ($n = 217$) per year on leopards *Panthera pardus*, using *ISI Web of Science* literature search from 1970–2010 (accessed on 13/04/2011; search string used: TS=((*Panthera pardus*) AND leopard) Timespan=All Years. Databases=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH).

In the past, leopard research has primarily been focused on both ecological and zoological studies interspersed with isolated case studies across the species' range. This trend still dominates leopard publications to date, suggested by an *ISI Web of Science* literature search from 1970–2011 (Fig. 2). At the turn of the century, scientific interest in leopards was boosted by the introduction of long-term, well-funded, leopard research projects like The Cape Leopard Trust (www.capeleopard.org.za) and Mun-Ya-Wana Leopard Project of the Panthera Foundation (www.panthera.org). The past ten years have seen a general increase in applied ecological research along with more conservation (Martins and Martins, 2006; Aljohany, 2007; Balme et al., 2009b), behavioural (de Ruiter and Berger, 2001), evolutionary (Zuberbühler and Jenny, 2002) and genetic studies (Kawanishi et al., 2010). Concerns about human-leopard interactions and the consequences thereof have led to more publications based around carnivore conflict management and mitigation, particularly concerning non-lethal management techniques like translocation (Schiess-Meier et al., 2007; Sangay and Vernes, 2008; Weilenmann et al., 2010; Athreya et al., 2011). The advent and cheaper cost of global positioning system (GPS) tracking devices and infrared camera traps have enhanced studies of cryptic species like leopards (Balme et al., 2009a; Swanepoel et al., 2010; Martins et al., 2011).

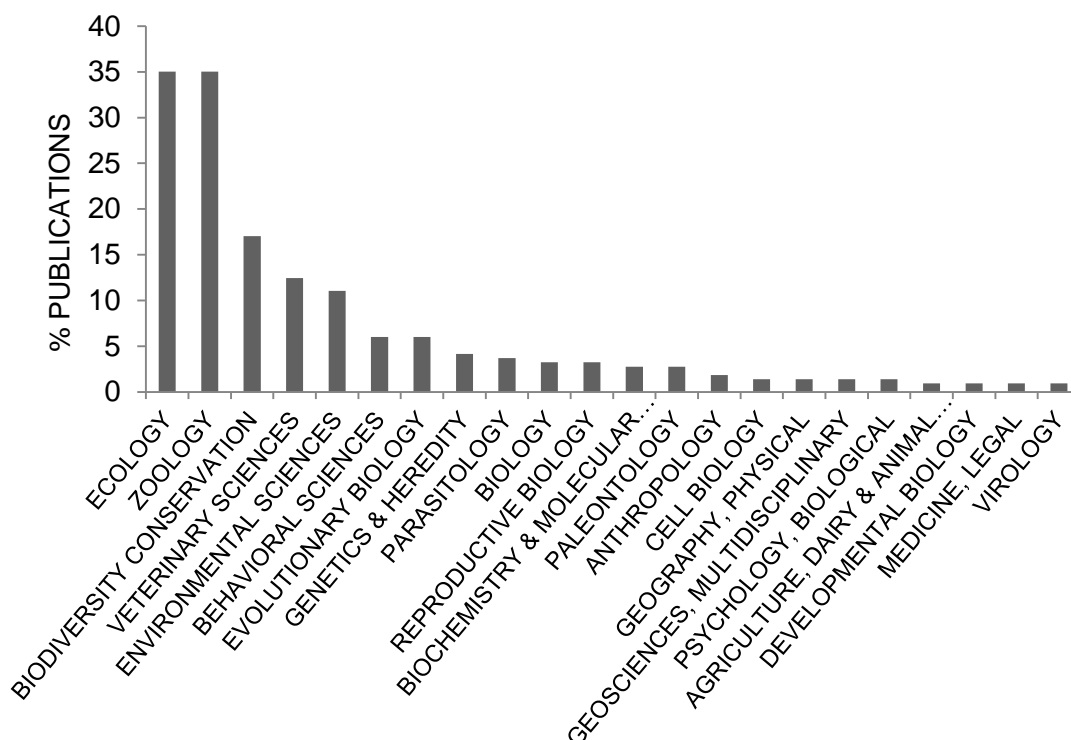


Figure 2: Percentage of publications ($n = 217$) based on—or including—leopards *Panthera pardus* using ISI Web of Science subject categories from 1970–2011 (accessed on 13/04/2011; search string used: TS=((Panthera pardus) AND leopard) Timespan=All Years. Databases=SCI-EXPANDED, SSCI, A&HCI, CPCI-S, CPCI-SSH).

Non-scientific, publically operated, leopard projects are spread throughout Africa, but particularly in South Africa (for example; www.leopardcon.co.za or www.ingweleopard.com). These organisations do not submit their findings to peer-reviewed journals; therefore it is possible that other areas of leopard research are being conducted, albeit on a strictly non-scientific basis.

Areas requiring research

To date, most studies have been carried out in savannah and forest ecosystems such as Serengeti National Park (Bertram, 1974), Phinda Private Game Reserve (Balme et al., 2007; Balme et al., 2010), the Kalahari desert (Bothma et al., 1997; Bothma and Bothma, 2006), and equatorial Africa (Jenny and Zuberbuhler, 2005; Henschel, 2008). These regions have allowed scientists to visually observe or track leopards on a continual basis. In areas of rugged, mountainous terrain studies are lacking (Martins et al., 2011). Very high frequency (VHF) radio collars have been used ever since the mid 1970's (Bertram, 1974). However, VHF telemetry is time-consuming (requires physical tracking), expensive, and only reliable in open areas (Norton and Lawson, 1985). The use of GPS or satellite based telemetry devices avoid the pitfalls of VHF telemetry by remotely collecting fine-scale data (Swanepoel et al., 2010). Research techniques that allow scientists to effectively monitor leopards in inaccessible ecosystems (e.g., mountains) are essential (Martins et al., 2011). Innovative GPS techniques like 'cluster analysis' have allowed scientists to remotely monitor predation (Anderson and Lindzey,

2003; Sand et al., 2005; Tambling et al., 2010). This technique requires validation for leopards in particular, but may offer a way to effectively monitor leopard predation in rugged areas. Due to the versatility of GPS collars, these studies not only focus on leopard feeding ecology, but also spatial distribution, species interactions and habitat use (Pitman et al., unpublished).

Understanding how leopards influence their environment is very important for their conservation, and the conservation of other species and habitats. Very little are known about the interactions between leopards and other carnivores, and particularly how the carnivore guild reacts to the loss (*i.e.*, extirpation, harvesting) of top predators like leopards (Ray et al., 2005). Also, herbivores live in a constant balance between maximizing nutrient intake and predator avoidance (*i.e.*, “landscape of fear”) (Broere, 2010), yet we are unaware of how leopards influence this dynamic relationship. Although baseline, single-species ecological studies are still necessary, coordinated research that incorporates multiple species is now desperately required (Ray et al., 2005).

Advances in camera trapping techniques and capture-recapture population modeling on tigers be can applied to leopard research on a large scale whilst incurring only minimal costs (Karanth and Nichols, 1998; Henschel, 2008; Balme, 2009; Balme et al., 2009a). This technique may be the only feasible way to reliably estimate worldwide population sizes of leopards, but would require a standardized approach and substantial funding.

The most essential aspect of leopard research that challenges scientists today is managing and/or mitigating the issues of human-leopard conflict[†]. During his literature search, Brodie (2009) totaled a mere 10 publications relating to human-leopard conflict over a 22-year time period. Although studies on human-leopard conflict are gaining popularity, more research on a broad scale needs to be done.

Research that investigates the effects of hunting, harvesting, translocations, and overall management of leopards (*e.g.*, similar to the work of Balme, Hunter & Slotow 2009) is required throughout Africa. These issues are controlled by local authorities and may, if necessary, require reevaluation and modifications to legislation.

Although phylogenetic research on leopards have been done, a more comprehensive study, that uses a larger sample size, is required (Uphyrkina et al., 2001). An understanding of the genetic diversity within leopard populations, on a large scale, is deficient within the primary literature. This lack of knowledge has implications for translocations (*i.e.*, unintentionally mixing the gene pool) and habitat loss (*e.g.*, loss of genetically unique, geographically isolated leopard species). Genetic studies, particularly in South Africa, are currently underway in the Limpopo and Cape Province[‡].

Although leopards are one of the top four most studied felids, many publications have not sufficiently dealt with their conservation and management in a changing, human-dominated landscape, particularly on a long-term basis. Research that encourages and demonstrates sustainable conservation practices of leopards and other carnivores, so

[†] Personal communication with Dr. Luke Hunter – President of Panthera Foundation, 8 West 40th Street, 18th Floor, New York, NY 10018, USA

[‡] Personal communication with Lourens Swanepoel – PhD candidate, University of Pretoria, Centre of Wildlife Management, Pretoria, South Africa

that not only the animals but also local communities benefit financially and socially, is needed to ensure long-term population viability.

References

- Abbasi, A. & Braunitzer, G. (1985) *The primary structure of hemoglobin from Amur leopard *Panthera pardus orientalis**. *Journal of Protein Chemistry*, **4**, 57–67.
- Ahmed, A., Jahan, M. & Braunitzer, G. (1988) *Carnivora - The primary structure of the major and minor hemoglobin components of adult North Persian leopard *Panthera pardus sexicolor**. *Zeitschrift Fur Naturforschung Section B - A Journal of Chemical Sciences*, **43**, 1341–1346.
- Aiello, L. C. & Wheeler, P. (1995) *The expensive tissue hypothesis: the brain and the digestive system in human and primate evolution*. *Current Anthropology*, **36**, 199–221.
- Aljohany, A. (2007) *Distribution and conservation of the Arabian leopard *Panthera pardus nimr* in Saudi Arabia*. *Journal of Arid Environments*, **68**, 20–30.
- Andelman, S. J. & Fagan, W. F. (2000) *Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences of the United States of America*, **97**, 5954–5959.
- Anderson, C. R. & Lindzey, F. G. (2003) *Estimating cougar predation rates form GPS clusters*. *Journal of Wildlife Management*, **67**, 307–316.
- Appel, M. J. G., Yates, R. A., Foley, G. L., Bernstein, J. J., Santinelli, S., Spelman, L. H., Miller, L. D., Arp, L. H., Anderson, M., Barr, M., Pearcekelling, S. & Summers, B. A. (1994) *Canine distemper epizootic in lions, tigers, and leopards in North America*. *Journal of Veterinary Diagnostic Investigation*, **6**, 277–288.
- Athreya, V., Odden, M., Linnell, J. D. & Karanth, K. U. (2011) *Translocation as a tool for mitigating conflict with leopards in human-dominated landscapes of India*. *Conservation Biology : The Journal of the Society for Conservation Biology*, **25**, 133–141.
- Bailey, T. N. (2005) *The African leopard: ecology and behavior of a solitary felid*, 2nd edn. The Blackburn Press, New Jersey.
- Balme, G. (2009) *The conservation biology of a nominally protected leopard population*. PhD, University of Kwa-Zulu Natal.
- Balme, G. A., Hunter, L. T. B. & Slotow, R. (2007) *Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance*. *Animal Behaviour*, **74**, 589–598.
- Balme, G. A., Hunter, L. T. B. & Slotow, R. (2009a) *Evaluating methods for counting cryptic carnivores*. *Journal of Wildlife Management*, **73**, 433–441.

- Balme, G. A., Slotow, R. & Hunter, L. T. B. (2009b) *Impact of conservation interventions on the dynamics and persistence of a persecuted leopard Panthera pardus population*. *Biological Conservation*, **142**, 2681–2690.
- Balme, G. A., Slotow, R. & Hunter, L. T. B. (2010) *Edge effects and the impact of non-protected areas in carnivore conservation: leopards in the Phinda-Mkhuze Complex, South Africa*. *Animal Conservation*, **13**, 315–323.
- Bertram, B. (1974) Radio-tracking leopards in the Serengeti. *African Wildlife Leadership Foundation News*, **9**, pp. 8–10.
- Blejwas, K. M., Sacks, B. N., Jaeger, M. M. & McCullough, D. R. (2002) *The effectiveness of selective removal of breeding coyotes in reducing sheep predation*. *Journal of Wildlife Management*, **66**, 451–462.
- Blumenschine, R. J. (1991) *Hominid carnivory and foraging strategies, and the socio-economic function of early archeological sites*. *Philosophical Transactions of the Royal Society of London*, **334**, 211-221.
- Bothma, I. D. & Bothma, M. D. (2006) *Activity patterns in southern Kalahari leopards*. *African Zoology*, **41**, 150–152.
- Bothma, J. D. & Coertze, R. J. (2004) *Scent-marking frequency in southern Kalahari leopards*. *South African Journal of Wildlife Research*, **34**, 163–169.
- Bothma, J. D., Knight, M. H., Le Riche, E. A. N. & van Hensbergen, H. J. (1997) *Range size of southern Kalahari leopards*. *South African Journal of Wildlife Research*, **27**, 94–99.
- Bothma, J. P. & Le Riche, E. A. N. (1984) *Aspects of the ecology and the behaviour of the leopard Panthera pardus in the kalahari desert*. *Koedoe*, 259–279.
- Bothma, J. P. & Le Riche, E. A. N. (1995) *Evidence of the use of rubbing, scent marking and scratching posts by Kalahari leopards*. *Journal of Arid Environments*, **29**, 511–517.
- Bourne, J. (2002) *Electric fencing for predator control in Alberta*. *Carnivore Damage Protection News*, **5**, 9–10.
- Brodie, J. F. (2009) *Is research effort allocated efficiently for conservation? Felidae as a global case study*. *Biodiversity and Conservation*, **18**, 2927–2939.
- Broere, M. (2010) *The landscape of fear: the trade-off between nutrients and predation risks for large African herbivores - A study in Welgevonden Private Game Reserve, South Africa*. MSc, Wageningen University.
- Caro, T. M. (2003) *Umbrella species: critique and lessons from East Africa*. *Animal Conservation*, **6**, 171–181.
- Caro, T. M. & Stoner, C. J. (2003) *The potential for interspecific competition among African carnivores*. *Biological Conservation*, **110**, 67–75.

- Cavallo, J. A. (1991) *A study of leopard behavior and ecology in the Seronera Valley, Serengeti National Park, Tanzania*. Serengeti Wildlife Research Institute, 1–20.
- Child, B. (2000) Application of the southern African wildlife experience to wildlife utilization in Kenya and Tanzania. *Wildlife Conservation by Sustainable Use*. Conservation Biology Series, London: Kluwer.
- CITES (2008) Export quotas for specimens of species included in the CITES Appendices for 2008.
- CoP-13 (2004) Leopard: export quota for South Africa. *Interpretation and implementation of the Convention: Thirteenth meeting of the Conference of the Parties Bangkok, Thailand*.
- Crooks, K. R. & Soule, M. E. (1999) *Mesopredator release and avifaunal extinctions in a fragmented system*. *Nature*, **400**, 563-566.
- Culver, M., Johnson, W. E., Pecon-Slattery, J. & O'Brien, S. J. (2000) *Genomic ancestry of the American puma Puma concolor*. *The American Genetic Association*, **91**, 186–197.
- Damm, G. (2005) *Hunting in South Africa: facts, risks and opportunities*. *African Indaba*, **3**, 1–14.
- de Ruiter, D. J. & Berger, L. R. (2001) *Leopard Panthera pardus cave caching related to anti-theft behaviour in the John Nash Nature Reserve, South Africa*. *African Journal of Ecology*, **39**, 396–398.
- Driscoll, C. A. (1998) A characterization of microsatellite loci variation in *Panthera leo*, *Acinonyx jubatus* and *Felis concolor*. MSc, Hood College, Frederick M.D.
- du Plessis, H. & Smit, G. N. (2001) The development and final testing of an electrified leopard proof game fence on the farm Masequa. University of the Free State.
- Eates, J., Crooks, K. & Holt, R. (2001) *Predation and diversity*. Encyclopedia of Biodiversity. Academic Press, San Diego CA, San Diego.
- Eates, J. A. & Duggins, D. O. (1995) *Sea otters and kelp forests in Alaska: generality and variation in a community ecology paradigm*. *Ecological Monographs*, **65**, 75-100.
- Eaton, R. L. (1978) *The conservation of the leopard in Africa: towards an authentic philosophy of conservation*. *Carnivore*, **1**, 82–149.
- Eizirik, E., Kim, J., Menotti-Raymond, M., Crawshaw Jr., P. G., O'Brien, S. J. & Johnson, W. E. (2001) *Phylogeography, population history and conservation genetics of jaguars (Panthera onca, Mammalia, Felidae)*. *Molecular Ecology*, **10**, 65–79.

- Elmhagen, B. & Rushton, S. P. (2007) *Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up?* *Ecology Letters*, **10**, 197-206.
- Grimbeek, A. M. (1992) The ecology of the leopard *Panthera pardus* in the Waterberg. MSc, University of Pretoria.
- Hamilton, P. H. (1981) The leopard *Panthera pardus* and the cheetah *Acinonyx jubatus* in Kenya. *The U.S. Fish and Wildlife Service*. The African Wildlife Leadership Foundation, Government of Kenya.
- Harder, T. C., Kenter, M., Vos, H., Siebelink, K., Huisman, W., van Amerongen, G., Orvell, C., Barrett, T., Appel, M. J. G. & Osterhaus, A. (1996) *Canine distemper virus from diseased large felids: biological properties and phylogenetic relationships*. *Journal of General Virology*, **77**, 397–405.
- Hayward, G. D., Miquelle, D. G., Smirnov, E. N. & Nations, C. (2002) *Monitoring Amur tiger populations: characteristics of track surveys in snow*. *Wildlife Society Bulletin*, **30**, 1150–1159.
- Henschel, P. (2008) The conservation biology of the leopard *Panthera pardus* in Gabon: status, threats and strategies for conservation. PhD, Georg-August-Universität zu Göttingen.
- Henschel, P., Hunter, L., Breitenmoser, U., Purchase, N., Packer, C., Khorozyan, I., Bauer, H., Marker, L., Sogbohossou, E. & Breitenmoser-Wursten, C. (2008) *Panthera pardus*. *IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4*.
- Henschel, P., Hunter, L. T. B., Coad, L., Abernethy, K. A. & Mühlenberg, M. (2011) *Leopard prey choice in the Congo Basin rainforest suggests exploitative competition with human bushmeat hunters*. *Journal of Zoology*, 1–10.
- Henschel, P. & Ray, J. (2003) Leopards in African rainforests: survey and monitoring techniques. *Wildlife Conservation Society, Global Carnivore Program*. New York, USA.
- Hoppedominik, B. (1984) *Prey frequency of the leopard Panthera pardus in the Tai-National Park of the Ivory Coast*. *Mammalia*, **48**, 477–487.
- Hunter, L., Henschel, P. & Ray, J. C. (in press) *Panthera pardus*. *The Mammals of Africa: carnivores, pangolins, rhinos, and equids*. Academic Press, Amsterdam, The Netherlands.
- Hutton, J. M. & Leader-Williams, N. (2003) *Sustainable use and incentive-driven conservation: realigning human and conservation interests*. *Oryx*, **37**.
- Ingman, M., Kaessmann, H., Paabo, S. & Gyllensten, U. (2000) *Mitochondrial genome variation and the origin of modern humans*. *Nature*, **408**, 708–713.
- Jackson, R. M., Roe, J. D., Wangchuk, R. & Hunter, D. O. (2006) *Estimating snow leopard population abundance using photography and capture-recapture techniques*. *Wildlife Society Bulletin*, **34**, 772–781.

- Jenny, D. (1996) *Spatial organization of leopards Panthera pardus in Tai National Park, Ivory Coast: is rain forest habitat a tropical haven?* *Journal of Zoology*, **240**, 427–440.
- Jenny, D. & Zuberbuhler, K. (2005) *Hunting behaviour in West African forest leopards*. *African Journal of Ecology*, **43**, 197–200.
- Johnson, K. G., Wang, W., Reid, D. G. & Hu, J. C. (1993) *Food habits of Asiatic leopards Panthera pardus fusea in Wolong Reserve, Sichuan, China*. *Journal of Mammalogy*, **74**, 646–650.
- Jorgenson, J. P. & Redford, K. H. (1993) *Humans and big cats as predators in the Neotropics*. *Symposia of the Zoological Society of London*, **65**, 367–390.
- Karanth, K. U. & Nichols, J. D. (1998) *Estimation of tiger densities in India using photographic captures and recaptures*. *Ecology*, **79**, 2852–2862.
- Karanth, K. U., Nichols, J. D., Seidenstricker, J., Dinerstein, E., Smith, J. L. D., McDougal, C., Johnsingh, A. J. T., Chundawat, R. S. & Thapar, V. (2003) *Science deficiency in conservation practice: the monitoring of tiger populations in India*. *Animal Conservation*, **6**, 141–146.
- Kawanishi, K., Sunquist, M. E., Eizirik, E., Lynam, A. J., Ngoprasert, D., Wan Shahrudin, W. N., Rayan, D. M., Sharma, D. S. K. & Steinmetz, R. (2010) *Near fixation of melanism in leopards of the Malay Peninsula*. *Journal of Zoology*, **282**, 201–206.
- Künzel, T., Rayaleh, H. A. & Künzel, S. (2000) *Status assessment on wildlife in Djibouti*. *Zoological Society for Conservation of Species and Populations*. Munich, Germany.
- Leroux, P. G. & Skinner, J. D. (1989) *A note on the ecology of the leopard Panthera pardus in the Londolozi Game Reserve, South Africa*. *African Journal of Ecology*, **27**, 167–171.
- Lindsey, P. A., Alexander, R., Du Toit, J. T. & Mills, M. G. L. (2005) *The cost efficiency of wild dog conservation in South Africa*. *Conservation Biology*, **19**, 1205–1214.
- Lindsey, P. A., Alexander, R., Frank, L. G., Mathieson, A. & Romanach, S. S. (2006) *Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable*. *Animal Conservation*, **9**, 283–291.
- Linnell, J. D. C., Smith, M. E., Odden, J., Kaczensky, P. & Swenson, J. E. (1996) *Strategies for the reduction of carnivore-livestock conflicts: a review*. *Norwegian Institute for Nature Research Oppdragmelding*, **443**, 1–118.
- Logan, K. A. & Sweanor, L. L. (2001) *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Island Press, Washington D.C.

- Loveridge, A., Searle, A., Murindagomo, F. & Macdonald, D. (2007) *The impact of sport-hunting on the population dynamics of an African lion population in a protected area. Biological Conservation*, **134**, 548–558.
- Macdonald, A. A. & Johnstone, M. (1995) *Comparative anatomy of the cardiac foramen ovale in cats (Felidae), dogs (Canidae), Bears (Ursidae), and Hyaenas (Hyaenidae). Journal of Anatomy*, **186**, 235–243.
- Martin, R. B. & de Meulenaer, T. (1988) Survey of the status of the leopard *Panthera pardus* in sub-Saharan Africa. *CITES Secretariat*. Lausanne, Switzerland.
- Martins, Q., Horsnell, W. G. C., Titus, W., Rautenbach, T. & Harris, S. (2011) *Diet determination of the Cape mountain leopards using global positioning system location clusters and scat analysis. Journal of Zoology*, **283**, 81–87.
- Martins, Q. & Martins, N. (2006) *Leopards of the Cape: conservation and conservation concerns. International Journal of Environmental Studies*, **63**, 579–585.
- Miller, B., Dugelby, B., Foreman, D., Martinez del Rio, C., Noss, R., Phillips, M., Reading, R., Soulé, M. E., Terborgh, J. & Willcox, L. (2001) *The importance of large carnivores to healthy ecosystems. Endangered Species Update*, **18**, 202–210.
- Mishra, C., Allen, P., McCarthy, T., Madhusudan, M. D., Bayarjargal, A. & Prins, H. H. T. (2003) *The role of incentive programs in conserving the snow leopard. Conservation Biology*, **17**, 1512–1520.
- Miththapala, S., Seidensticker, J. & Obrien, S. J. (1996) *Phylogeographic subspecies recognition in leopards Panthera pardus: molecular genetic variation. Conservation Biology*, **10**, 1115–1132.
- Mizutani, F. (1999) *Impact of leopards on a working ranch in Laikipia, Kenya. African Journal of Ecology*, **37**, 211–225.
- Myers, N. (1976) *The leopard Panthera pardus in Africa. IUCN Monograph No. 5. Morges, Switzerland.*
- Norton, P. (1990) *How many leopards? A criticism of Martin and de Meulenaer's population estimates for Africa. South African Journal of Science*, **86**, 218.
- Norton, P. M. & Lawson, A. B. (1985) *Radio tracking of leopards and caracals in the Stellenbosch area, Cape Province. Suid-Afrikaanse Tydskrif vir Natuurwetenskap en Tegnologie*, **15**, 17–24.
- Nowell, P. M. & Jackson, P. (1996) *Wild Cats: Status, survey and conservation action plan*. Burlington Press, Cambridge.

- Nyhus, P. J., Osofsky, S. A., Ferraro, P., Madden, F. & Fischer, H. (2005) Bearing the human-wildlife conflict: the challenges of compensation schemes. *People and wildlife: conflict or co-existence*, pp. 107–121. Cambridge University Press, Cambridge.
- Odden, J., Linnell, J. D. C. & Moa, P. F. (2002) *Lynx depredation on domestic sheep in Norway*. *Journal of Wildlife Management*, **66**, 98–105.
- Ogada, M. O., Woodroffe, R., Ouge, N. & Frank, L. G. (2003) *Limiting depredation by African carnivores: the role of livestock husbandry*. *Conservation Biology*, **17**, 1521–1530.
- Packer, C., Brink, H., Kissui, B. M., Maliti, H., Kushnir, H. & Caro, T. (2011) *Effects of trophy hunting on lion and leopard populations in Tanzania*. *Conservation Biology*, **25**, 142–153.
- Packer, C., Kosmala, M., Cooley, H. S., Brink, H., Pintea, L., Garshelis, D., Purchase, G., Struass, M., Swanson, A., Balme, G., Hunter, G. & Nowell, K. (2009) *Sport hunting, predator control and conservation of large carnivores*. *PLoS ONE*, **4**, 1–8.
- Patterson, B. (2004) *Livestock predation by lions *Panthera leo* and other carnivores on ranches neighboring Tsavo National Park, Kenya*. *Biological Conservation*, **119**, 507–516.
- Patton, S. & Rabinowitz, A. R. (1994) *Parasites of wild Felidae in Thailand - a coprological survey*. *Journal of Wildlife Diseases*, **30**, 472–475.
- Pikunov, D. G. & Korkishko, V. G. (1985) *The present distribution and numbers of leopards *Panthera pardus* in the Soviet Far-East*. *Zoologicheskyy Zhurnal*, **64**, 897–905.
- Pitman, R. T., Swanepoel, L. H. & Ramsay, P. (unpublished) *Predictive modelling of leopard *Panthera pardus* predation using contextual GPS cluster analysis*.
- Pocock, R. I. (1930) *The panthers and ounces of Asia*. *Journal of Bombay Natural History Society*, **XXXIV**, 63–82; 307–336.
- Pocock, R. I. (1932) *The leopards of Africa*. *Proceedings of Zoological Society of London*, 543–591.
- Pozio, E., DeMeneghi, D., RoelkeParker, M. E. & LaRosa, G. (1997) *Trichinella nelsoni in carnivores from the Serengeti ecosystem, Tanzania*. *Journal of Parasitology*, **83**, 1195–1198.
- Rabinowitz, A. (1986) *Jaguar predation on domestic livestock in Belize*. *Wildlife Society Bulletin*, **14**, 170–174.
- Ray, J. C. (2001) Carnivore biogeography and conservation in the African forest: A community perspective. *African Rainforest Ecology and Conservation - An Interdisciplinary Perspective*, pp. 214-232. Yale University Press, New Haven.

- Ray, J. C., Hunter, L. & Zigouris, J. (2005) *Setting conservation and research priorities for large African carnivores*. Wildlife Conservation Society, New York.
- Ray, S., Ray, M., Mandal, S. C. & Dutta, G. K. (1997) *Anatomy of the humerus of leopard Panthera pardus*. *Indian Journal of Animal Sciences*, **67**, 131–131.
- Ray, S., Ray, M., Mandal, S. C., Dutta, G. K. & Das, K. (1996) *Anatomical study of the femur (os femoris) of leopard Panthera pardus*. *Indian Journal of Animal Sciences*, **66**, 147–148.
- Redfern, J. V., Viljoen, P. C., Kruger, J. M. & Getz, W. M. (2002) *Biases in estimating population size from an aerial census: a case study in the Kruger National Park, South Africa*. *South African Journal of Science*, **98**, 455-461.
- Ritchie, E. G. & Johnson, C. N. (2009) *Predator interactions, mesopredator release and biodiversity conservation*. *Ecology Letters*, **12**, 982-998.
- Rondeau, D. & Bulte, E. (2007) *Wildlife Damage and Agriculture: a dynamic analysis of compensation schemes*. *American Journal of Agricultural Economics*, **89**, 490–507.
- Roychoudhury, A. K. & Achariyo, L. N. (1984) *Genetics of coat color in the leopard Panthera pardus*. *Indian Journal of Experimental Biology*, **22**, 308–311.
- Sand, H., Zimmermann, B., Wabakken, P., Andr  n, H. & Pedersen, H. C. (2005) *Using GPS technology and GIS cluster analyses to estimate kill rates in wolf–ungulate ecosystems*. *Wildlife Society Bulletin*, **33**, 914–925.
- Sangay, T. & Vernes, K. (2008) *Human-wildlife conflict in the Kingdom of Bhutan: patterns of livestock predation by large mammalian carnivores*. *Biological Conservation*, **141**, 1272–1282.
- Santiapillai, C., Chambers, M. R. & Ishwaran, N. (1982) *The leopard Panthera pardus fusca (Meyer 1794) in the Ruhuna National Park, Sri Lanka, and observations relevant to its conservation*. *Biological Conservation*, **23**, 5–14.
- Savarie, J. & Sterner, R. T. (1979) *Evaluation of toxic collars for selective control of coyotes that attack sheep*. *Journal of Wildlife Management*, **43**, 780–783.
- Schiess-Meier, M., Ramsauer, S., Gabanapelo, T. & Konig, B. (2007) *Livestock predation - insights from problem animal control registers in Botswana*. *Journal of Wildlife Management*, **71**, 1267–1274.
- Shipp, A. (2002) *Wildlife for sale in Marrakech, Morocco*. *Traffic Bulletin*, **19**, 65.
- Shivik, J. A. (2006) *Tools for the edge: what's new for conserving carnivores*. *Bioscience*, **56**, 253–259.
- Shoemaker, A. H. (1985) *1983 Studbook for rare leopards Panthera pardus*. *Zoo Biology*, **4**, 169–196.

- Singh, H. S. (2005) *Status of the Leopard Panthera pardus fusca in India*. *Cat News*, **42**, 15–17.
- Soulé, M. E. & Terborgh, J. (1999) The role of top carnivores in regulating terrestrial ecosystems. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Island Press.
- Spong, G., Hellborg, L. & Creel, S. (2000) *Sex ratio of leopards taken in trophy hunting: genetic data from Tanzania*. *Conservation Genetics*, **1**, 169–171.
- Stander, P. E. (1997) *Field age determination of leopards by tooth wear*. *African Journal of Ecology*, **35**, 156–161.
- Stander, P. E., Kagece, a., Nisa, a., Dabe, T. & Dabe, D. (1997) *Non-consumptive utilisation of leopards community conservation and ecotourism in practise*. *Onderstepoort*, 50–56.
- Stoner, D. C., Wolfe, M. L. & Choate, D. M. (2006) *Cougar exploitation levels in Utah: Implications for demographic structure, population recovery, and metapopulation dynamics*. *Journal of Wildlife Management*, **70**, 1588–1600.
- Stuart, C. T. & Stuart, T. D. (1993) *Prey of leopards in the western Soutpansberg, South Africa*. *Journal of African Zoology*, **107**, 135–137.
- Swanepoel, L. H. (2009) Ecology and conservation of leopards *Panthera pardus* on selected game ranches in the Waterberg region, Limpopo, South Africa. MSc, University of Pretoria.
- Swanepoel, L. H., Dalerum, F. & van Hoven, W. (2010) *Factors affecting location failure of GPS collars fitted to African leopards Panthera pardus*. *South African Journal of Wildlife Research*, **40**, 10–15.
- Tambling, C. J., Cameron, E. Z., Du Toit, J. T. & Getz, W. M. (2010) *Methods for locating African lion kills using global positioning system movement data*. *Journal of Wildlife Management*, **74**, 549–556.
- Teer, J. B. & Swank, W. G. (1977) Status of the leopard in Africa south of the Sahara. *U.S. Fish and Wildlife Service*. Washington, D.C.
- Thorel, M. F., Karoui, C., Varnerot, A., Fleury, C. & Vincent, V. (1998) *Isolation of mycobacterium bovis from baboons, leopards and a sea-lion*. *Veterinary Research*, **29**, 207-212.
- Tilde, C. & Tilde, S. (1988) *Leopard in the lower Orange River basin - a study of their conservation status*. *African Carnivore Survey*.
- Treves, A. & Karanth, K. U. (2003) *Human-carnivore conflict and perspectives on carnivore management worldwide*. *Conservation Biology*, **17**, 1491–1499.
- Treves, A. & Naughton-Treves, L. (2005) Evaluating lethal control in the management of human-wildlife conflict. *People and wildlife: conflict or wildlife*, pp. 86–106. Cambridge University Press, Cambridge.

- Tuytens, F. A. M. & Macdonald, D. W. (1998) *Fertility control: an option for the non-lethal control of wild carnivores?* *Animal Welfare*, **7**, 339–364.
- Uphyrkina, O., Johnson, W. E., Quigley, H., Miquelle, D., Marker, L., Bush, M. & O'Brien, S. J. (2001) *Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus**. *Molecular Ecology*, **10**, 2617–2633.
- Weilenmann, M., Gusset, M., Mills, D. R., Gabanapelo, T. & Schiess-Meier, M. (2010) *Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool?* *Wildlife Research*, **37**, 702–707.
- Wielgus, R. B. & Bunnell, F. L. (2000) *Possible negative effects of adult male mortality on female grizzly bear reproduction*. *Biological Conservation*, **93**, 145–154.
- Williams, B. K., Nichols, J. D. & Conroy, M. J. (2002) *Analysis and management of animal populations: modeling, estimation, and decision making*. Academic Press, London, England.
- Woodroffe, R. (2000) *Predators and people: using human densities to interpret declines of large carnivores*. *Animal Conservation*, **3**, 165–173.
- Woodroffe, R. & Ginsberg, J. R. (1998) *Edge effects and the extinction of populations inside protected areas*. *Science*, **280**, 2126–2128.
- Zuberbühler, K. & Jenny, D. (2002) *Leopard predation and primate evolution*. *Journal of Human Evolution*, **43**, 873–886.